Biodivers Conserv (2013) 22:2937–2956
DOI 10.1007/s10531-013-0564-7

ORIGINAL PAPER

Density and habitat use of lions and spotted hyenas in northern Botswana and the influence of survey and ecological variables on call-in survey estimation

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Received: 16 October 2012 / Accepted: 13 September 2013 / Published online: 26 September 2013

Abstract Top predators significantly impact ecosystem dynamics and act as important indicator species for ecosystem health. However, reliable density estimates for top predators, considered necessary for the development of management plans and ecosystem monitoring, are challenging to obtain. This study aims to establish baseline density estimates for two top predators, spotted hyena and lion, in the Okavango Delta in northern Botswana. Using calling stations, we surveyed free-ranging populations of the two species and investigated methodological variables that might influence results about distributions and densities, including habitat type, seasonality, and different types of playback sounds. Calling stations were distributed over a survey area of approximately 1,800 km^2 characterized by three major habitat types: mopane woodland, floodplain and mixed acacia sandveld. Results indicate spotted hyenas were evenly distributed independent of habitat type and season throughout the survey area with an overall density estimate of 14.4 adults/100 km^2. In contrast, lion distribution and density varied significantly with habitat and season. Lion density in the prey-poor mopane woodland was near zero, while in the comparatively prey-rich floodplains it was estimated at 23.1 individuals/100 km^2 resulting in a weighted average density of 5.8 individuals/100 km^2 across the entire study area. In testing the effect of varying playback sounds we found that both species were significantly more likely to respond to calls of conspecifics. Our results show how several

Electronic supplementary material The online version of this article (doi:10.1007/s10531-013-0564-7) contains supplementary material, which is available to authorized users.

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methodological variables may influence density estimates and emphasize the importance of standardized calling-station survey methods to allow consistent replication of surveys and comparison of results that can be used for landscape-scale monitoring of large predator species.

Keywords Calling-station · *Crocuta crocuta* · Density estimate · Habitat use · *Panthera leo* · Playback sounds

Introduction

The effective implementation of conservation strategies and management plans requires systematic assessment of the resources and biodiversity of an ecosystem (Gros et al. 1996; Ogutu and Dublin 1998; Mills et al. 2001; Kiffner et al. 2007; Funston et al. 2010). Reliable density estimates of animal and plant species are necessary, for example, to set sustainable harvesting quotas. Numerous direct and indirect methods to monitor wildlife populations and evaluate trends and changes have therefore been developed, but their utility and effectiveness varies, for example, with species, size and behaviour, and habitat type. Methods such as aerial surveys and line transects (e.g. Buckland et al. 1993; Jachmann 2002; Ogutu et al. 2006), regularly used to survey herbivore species, are generally inappropriate for species that are nocturnal, elusive or occur at low densities like most carnivore species. Consequently, alternative methodologies to assess the distribution and density of carnivore species have been developed (e.g. Harrington and Mech 1982; Karanth and Nichols 1998; Stander 1998; Balme et al. 2009).

For terrestrial carnivores, spoor surveys are widely recognized as a cost-effective broad-scale method for estimating distribution and densities of difficult to observe species, but their efficacy is substrate- and habitat-specific, making comparisons between survey areas/sites difficult (Stander 1998, but see Funston et al. 2010). Camera trapping is rapidly gaining acceptance for estimating populations of large carnivores (Karanth et al. 2006; Stein et al. 2008; Balme et al. 2009; Pettorelli et al. 2010). However, this methodology and its associated statistical treatment has not been developed for social group-living animals such as spotted hyenas *Crocuta crocuta* and lions *Panthera leo*. Furthermore, estimating densities requires identification of single individuals which is rarely possible for lions from camera-trap photos because close-up photographs of whiskers spot patterns are required to identify individual lions. A potentially less biased method to assess distribution and density of elusive carnivores on a broad scale is the calling-station survey, where broadcast playback recordings are used to elicit a response of target species. Because density estimates are based on the number of individuals responding to broadcast calls, the use of calling stations is particularly suitable for vocal, territorial species such as spotted hyenas and lions. Calling stations have several advantages in comparison to other techniques, including limited equipment, time (multiple calling stations can be conducted in a night) and skills/training requirements. Furthermore, calling-station surveys can be conducted in various landscapes independent of substrate and habitat and across large areas.

Calling stations have been used to investigate spatial and temporal variation in density and distribution across heterogeneous landscapes and habitats. For example, Mills et al. (2001) used calling stations to compare the distribution of hyenas in different vegetation types. Since Kruuk (1972) first used calling stations to survey spotted hyenas in the Serengeti, the method has been refined and applied for wider use elsewhere in widely varying habitats (e.g. Mills 1985; Ogutu and Dublin 1998; Mills et al. 2001; Creel and

Creel 2002; Winterbach et al. 2002; Kiffner et al. 2007). However, if this survey method is to be useful for comparisons among habitats, regions, and countries, a more rigorous standardisation of several methodological variables (e.g. broadcasting volume and types of calls broadcast) is required.

Because different calls convey different messages, the type of call used is likely to influence an animal's response. For example, the calls of an unknown female lion are expected to attract males as well as territorial females, which can be anticipated to approach to chase the intruder away (McComb et al. 1994; Grinnell and McComb 2001; Ramsauer 2005; Pfefferle et al. 2007). Female lion calls played to hyenas should leave them indifferent and not attract them, or may even partially deter them from approaching because of the presence of a larger and stronger competitor (Kiffner et al. 2007) unless the sound of prey or competition over food are involved. Kiffner et al. (2007) suggested that species-specific sounds should be played when using calling stations for hyenas or lions, but the degree to which different sounds influence response has not yet been tested. Other aspects, such as individual age and social status, group size and behaviour, may further influence response and need to be considered. For instance, lions on a kill very rarely responded to broadcast calls (Ogutu and Dublin 1998).

We used multiple calling stations over a 4-year period to estimate densities of free-ranging populations of spotted hyenas and lions in the Moremi Game Reserve (MGR) and adjacent Wildlife Management Areas (WMAs) in northern Botswana. For these regions, no previous density estimates were available for spotted hyenas, and the most recent estimates for lions were made in 2000 (Winterbach et al. 2002). In the present study, we aimed to establish new and more precise estimates for these two top predator species to establish baseline estimates for management purposes and future comparisons. Furthermore, we aimed to contribute to further standardization of calling-station surveys by investigating the effects of various survey variables. We conducted surveys across three major habitat types and sampled during both the wet and the dry season. We also investigated the responses of hyenas and lions to two distinct types of calls. Finally, we used cumulative location data collected daily from GPS radio-collared individuals to compare and validate the results of patterns of habitat use and distribution that emerged from the calling-station survey. Additionally, to validate our lion population estimates, we compared our calling-station estimates with independent information on individually recognized lions within our study area.

Materials and methods

Study area

We conducted our study in the Okavango Delta in northern Botswana, between 2007 and 2010, over an area of approximately 1,800 km^2 that comprised the eastern section of MGR and the adjacent WMAs (Fig. 1). MGR is not fenced and animals can move freely between the reserve and the WMAs, where the only permitted human activities are photographic and trophy-hunting (mainly elephants *Loxodonta africana*) tourism. Trophy hunting has been shown to negatively affect populations of wild lions (Loveridge et al. 2007; Becker et al. 2013). In Botswana, however, lion hunting was banned in 2000 and shortly resumed in 2005 prior to a definitive ban in 2007, and only one male lion was shot within the study area during the period 2005–2007. Therefore, we assumed that lion hunting in the study area was likely to have had a minor direct impact on lion density and response rate during

this study. The southern boundary of the study area is delimited by an artificial veterinary fence built to control the movements of Cape buffalo *Syncerus caffer* (Fig. 1).

The Okavango Delta is a freshwater ecosystem characterized by a mosaic of habitat types including rivers, swamps, perennial floodplains, seasonal floodplains, grassland, shrub-grassland, grassland dominated by *Acacia* trees, riparian woodland and woodland dominated by mopane (*Colophospermum mopane*) (Mendelson et al. 2010) (Fig. 1). We merged the different habitats of the Delta into three major habitat types: (1) mopane woodland, (2) floodplains (rivers, swamps, perennial floodplains and seasonal floodplains), and (3) mixed acacia sandveld, which comprised all remaining small fragments habitat types (grassland, shrub-grassland, riparian woodland and acacia-dominated grassland) (Fig. 1). Mopane woodland, floodplains and mixed sandveld represented, respectively, 53, 10 and 37 % of the entire 1,800 km^2 study area. We additionally defined a core area of 980 km^2 (Fig. 1), which was used by lions and spotted hyenas fitted with GPS radio collars. All resident lions within the core area could be individually recognized, but no such information was available for spotted hyenas. Mopane woodland, floodplains and mixed sandveld represented, 27, 11 and 62 % of the core area respectively.

The different habitat types support different prey species. In general, prey abundance is higher on floodplains and the associated riverine vegetation and lower in the mopane woodland, especially during the dry season (Bartlam 2010; Broekhuis 2012). The region is characterized by a dry season between April and October and a wet season between November and March, with average precipitation of 450–600 mm/year (Mendelson et al. 2010).

GPS collar data

Fifteen spotted hyenas in 7 clans and 14 lions in 6 prides resident within the core study area were fitted with GPS radio collars. A minimum of one and a maximum of four individuals were collared in each group over time (for more details see Table S1). Individuals to be collared were found by intensively searching for any sings of activity (e.g. spoor tracking, report from tourists and hunters, opportunistic sightings) starting form the centre of the core study area (where the research camp was situated). As individuals were progressively collared in adjacent territorial groups, we radially extended the search for additional neighbouring groups and individuals to be collared. As required by law, animals were immobilized by a qualified veterinarian using approved techniques and drug combinations (Kock et al. 2006). One GPS location was recorded every 2 h between 18:00 and 06:00 and one location was recorded at midday, giving a total of eight locations per day. On average, collars successfully recorded 84.8 ± 3.20 % (mean ± SEM) of the scheduled locations. A mean of 2,747 location per individual (range 395–9,450 locations) were collected for hyenas and a mean of 3,425 locations per individual (range 439–7,339 locations) were collected for lions.

Habitat data and calling-station sites

Eighteen calling-station sites were distributed equally within the three major habitat types (Fig. 1). The locations of the 'floodplain' sites were chosen to include a conspicuous percentage (>10 %) of floodplains within a 3 km radius. Where no floodplains were present with a 3 km radius, a site was categorized as 'mopane' or 'mixed' if more than 2/3 of the area within a 3 km radius was covered by mopane woodland or mixed acacia sandveld, respectively. The percentage of each vegetation type within a 3 km radius from the calling station site was calculated in ArcGIS 9.2 (ESRI) using a digital vegetation map

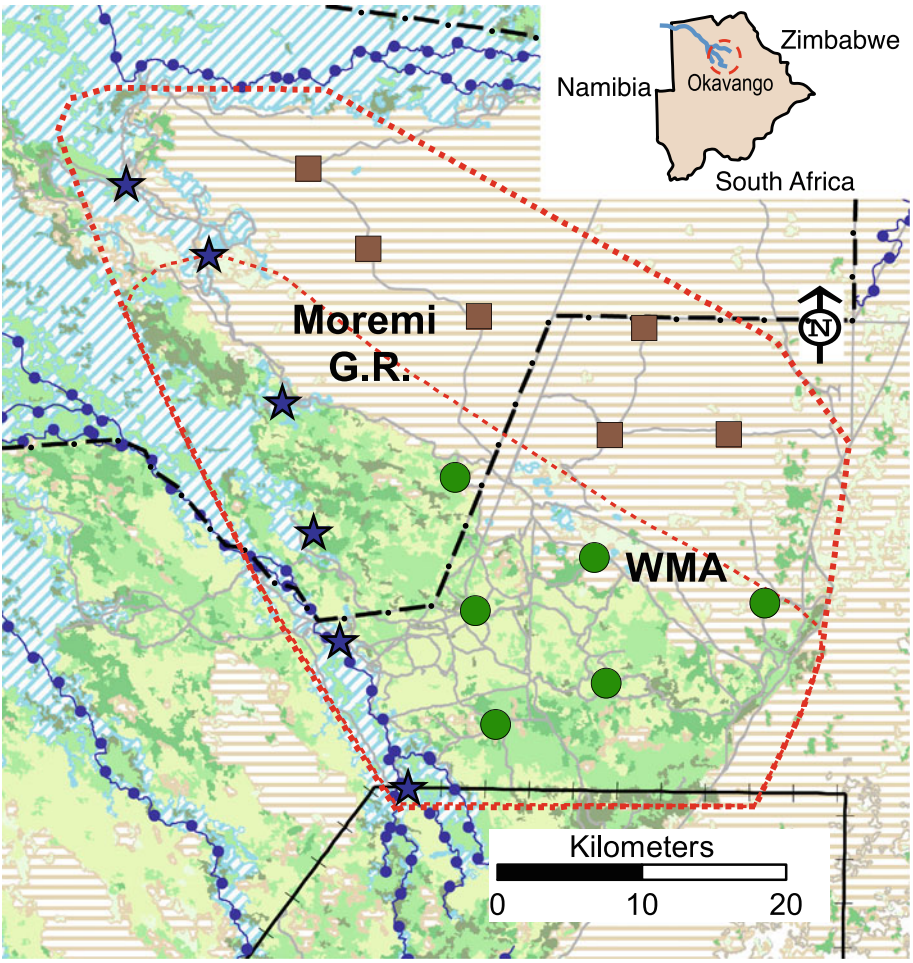

Fig. 1 The main study area of 1,800 km^2 (outer, *red dotted line*; see also inset map) was situated in the Okavango Delta in northern Botswana and comprised a section of MGR (*dashed-dotted line*) and the adjacent WMAs. This area was expanded from a 980 km^2 core area (inner, *red dotted lines*), which was used by GPS collared individuals, to include the calling-station sites located in the mopane woodland (*brown horizontal hatch*). The southern boundary of the study area was defined by the Southern Buffalo Fence (*ticked line*). Eighteen calling-station sites were sub-divided across three major habitat types on a 7 by 7 km grid and moved to the closest suitable road: six stations (*dark blue stars*) were located in the vicinity of floodplains (*pale blue oblique hatch*), six stations (*green circles*) in mixed sandveld (*shades of green* represent different vegetation types) and six stations (*brown quadrants*) in the mopane woodland (*brown horizontal hatch*). *Blue lines* represent rivers; *grey lines* roads; and the *inner red dotted line* a core area where all resident lions were individually recognized (see text for more details). (Color figure online)

provided by the Okavango Research Institute of the University of Botswana. For each site, the distance to the closest camping ground or lodge, the distance to perennial water (natural or artificial) and the distance to the veterinary fence were also calculated (Table S2). The 18 calling-station sites were roughly positioned on the intersection points of a rectangular 7 × 7 km grid. This distance was used to minimize the chances that an individual could hear playback sounds from more than one calling station at the same time and was based on

reports from Mills et al. (2001) and Creel and Creel (2002) and on results from calibration experiments conducted during this study. The exact location of each site was adjusted to obtain the best possible visibility, which was ≥50 m in all selected locations.

Calling-station survey

Calling-stations (=surveys) were used at night, starting at least half an hour after sunset, when hyenas and lions were mostly active (Cozzi et al. 2012). The surveys were conducted under bright moonlight conditions to facilitate the detection of approaching individuals whose silhouette was usually detectable without the need of additional artificial light. Minimizing the use of spotlights (i.e. to rapidly scan for eye-shine at regular intervals and, when necessary, for individual identification) helps to avoid repelling skittish individuals. Surveys were only conducted in the absence of wind; at the beginning of each survey the time and the temperature were recorded. Typically, 3–4 calling-station sites were surveyed within 1 night, and consequently 1 sampling round of all 18 sites lasted less than 7 nights, which was important to minimize the effect of potentially confounding environmental and ecological variables. All predator species approaching the calling-station sites during the surveys were recorded, as well as the time since the beginning of the survey. If possible, gender and age of each individual were noted. To investigate seasonal differences, surveys were conducted at the end of the rainy season (April–May) and at the end of the dry season (October–November) and all 18 sites were surveyed in both seasons.

Playback sounds

Animals were attracted to the calling station sites by means of playback sounds broadcast at 110 dB (measured at 1 m from the speaker with a PCE-EM882 digital Environmental Meter) through an Apple iPod attached to a 12 Volt Pioneer GM-X332 amplifier connected to an Electrovoice Sx500+ speaker positioned at 1.5 m above ground. During the broadcasting of the playback sounds, the speaker was rotated by 90° every 90 s to ensure 360° sampling (Ogutu and Dublin 1998; Mills et al. 2001; Kiffner et al. 2007).

We used two different sets of calls to test the response of hyenas and lions to different playback sounds. One set of calls, expected to be particularly suitable for attracting hyenas and successfully used for this purpose (Mills 1998; Mills et al. 2001; Creel and Creel 2002), consisted of several sounds representing the distress bleating of a wildebeest (*Connochaetes taurinus*) calf, hyenas competing over a kill, a fight between two neighbouring hyena clans and hyenas mobbing lions (the latter were not audible). In this paper we refer to this set of calls, which collectively lasted 6 min, as 'hyena calls'. The second set of calls, referred to as 'lion calls', consisted of the roars of a single lioness, distress calls of buffalo and hippopotamus (*Hippopotamus amphibious*), the distress bleating of a wildebeest calf and hyenas mobbing lions; these calls collectively lasted 10 min. Under the assumption that distress calls of different prey species will equally attract hungry predators, the main difference between these two sets of calls was the addition of the roar of a single female lion. We thus expected that the second set of calls would be particularly successful in attracting lions. The combinations of the playback sounds used were chosen to attempt to eliminate potential bias introduced by attracting only hungry individuals, as any resident individual should be attracted to social circumstances such as a territorial dispute or a single intruder (Mills et al. 2001).

No more than one sampling round of the 18 stations (lasting less than 7 nights) using the same set of calls (i.e. hyena calls or lion calls) was carried out per season to minimize

habituation of animals to the calls (Table S3). In those years where both hyena calls and lion calls were used during the same season (2008 and 2010, see Table S3), a time span of a month was allowed between the two rounds of the 18 stations.

Calibration experiments: broadcasting time and response likelihood

During calling-station surveys, an appropriate broadcasting time is necessary to (1) avoid that individuals which are located outside the auditory range would (e.g. per chance alone or because attracted by the calls of group members) walk within the auditory range and only then be attracted towards the speaker by the broadcasted calls and (2) allow enough time for individuals within the auditory range to approach the speaker. Violation of these two scenarios would inevitably increase (#1) or decrease (#2) the area sampled and bias density estimates. In other words, broadcasting time has to be long enough to allow individuals within the auditory range to approach and, at the same time, short enough to prevent individuals outside the auditory range to approach. Given the differences between hyenas and lions in their displacement speed, response distance, and reaction time to playback sounds (Ogutu and Dublin 1998; Kiffner et al. 2007; Maddox 2003, this study), broadcasting time needs to be species-specific and needs to be matched with an appropriate sampling radius. Even when a correct broadcasting time has been identified, not all individuals within the sampling range are, however, likely to approach (Ogutu and Dublin 1998; Mills et al. 2001). This response likelihood may, for instance, be a function of the distance to the speaker or of an animal's motivation, social status or reproductive status.

We therefore conducted 27 calibration experiments at varying distances (Table S4) to (1) determine the appropriate broadcasting time for the main calling-station surveys and (2) determine the likelihood that animals hearing the playback sound would actually approach (response likelihood). Calibration experiments could only be done for lions because in the study area hyenas were not accustomed to vehicles and it was therefore not possible to observe them during a calibration experiment without influencing their behaviour. Only 'lion calls' were therefore used for the calibration experiments.

Calibration experiments were carried out following the same protocol as the calling-station survey, with the only difference that the location of the target individual(s), and hence its distance to the speaker, was known. For this, the target individual(s) was located by means of traditional VHF telemetry during the day. During the calibration experiments one researcher was stationed with the target individual(s), while a second researcher played the playback sounds at an a priori set distance. Based on results from previous studies (Ogutu and Dublin 1998; Maddox 2003), calibration experiments were conducted at distances that ranged between 450 m and 3.1 km (Table S4). The calibration experiments were conceived to equally survey animal responses within the three habitat types. However, because of the very low abundance of lions in the mopane woodland (this study) and the difficulty in finding them in this habitat type, only three calibration experiments could be conducted in mopane (Table S4). The responses of the target individual(s) were noted and classified in a dichotomous way as response (vs. no response) if the target individual stopped its activity and paid attention to the calls and approach (vs. no approach) if the animal was observed at the calling station. Group size and behaviour of the target individual(s) were recorded, as well as the time taken to arrive at the calling station.

We used a linear model to analyse the relationship between response time and distance to the speaker. This information was then used to determine, for a given distance, the adequate broadcasting time for the main calling-station survey. Because we expected that with increasing distance between the lions and the speaker the variance in the time taken to

approach would increase (thus violating the assumption of homoscedasticity), we used a generalized least squares model with 'varExp' variance structure to account for the heteroscedasticity of the data (Zuur et al. 2009). The analyses were performed using the software R 2.13.0 for Windows (R Development Core Team 2011).

We used a logistic regression to infer the lions' response likelihood as a function of the distance to the speaker. The result of this regression analyses was used to assign a specific response likelihood to a specific distance, and to calculate the average response likelihood over the entire sampling radius surrounding each calling station.

Density estimates

We used data on the number of individuals approaching the calling stations (# individuals approaching); the distance at which animals responded to the calls to calculate the area sampled around each station (sampling area), and the likelihood of animals approaching (response likelihood) to calculate density estimates for the three habitat types and for the entire study area. Accordingly, we used the following formula:

$$\text{Density} = \frac{\#\text{ individuals approaching}}{\text{sampling area} \times \text{response likelihood}} \quad (1)$$

For lions, the results from the calibration experiments (see 'Calibration experiments' in "Results" section) suggested that a broadcasting time of 60 min (accordingly, the 10-min-long lion calls were separated by 5 min intervals of silence and repeated 4 times) was necessary to allow lions to approach from 2 km. Using 2 km as response distance yielded a sampling area of 12.6 km^2 around each calling station. Following the assumption that animals were evenly distributed over the sampling range (0–2 km) around each calling station site, we used a mean response likelihood of $\mu_{Li} = 0.6$. This mean value was calculated as the average of the response likelihoods across the sampling range 0–2 km (response likelihoods varied, for example, from 0.9 at 500 m to 0.4 at 2 km; for further details see 'Calibration experiments' in "Results" section).

Because we could not calibrate response distance and likelihood experimentally for hyenas, we used values from other studies. In the Kruger National Park, Mills et al. (2001) considered the response probability up to 3.2 km to be a constant and to be zero beyond that. Surveys in Hluhluwe-iMfolozi Park (Graf et al. 2009) and Selous Game Reserve (Creel and Creel 2002) both considered a response distance of 2.8 km to provide best estimates. We therefore used the mean of these three values [(3.2 km + 2.8 km + 2.8 km)/3 = 2.93 km] as our response distance, giving a sample area of 27.0 km^2 around each calling station. Response likelihood was estimated in Kruger National Park (Mills et al. 2001) and Hluhluwe-iMfolozi Park (Graf et al. 2009) at 0.61 and 0.60, respectively. For spotted hyenas, we used a response likelihood of $\mu_{SH} = 0.6$ at a distance of 2.9 km. Following Mills et al. (2001), Creel and Creel (2002) and Graf et al. (2009) broadcasting time was set to 30 min (accordingly, the 6-min-long hyena calls were separated by 4 min intervals of silence and repeated 3 times). For hyenas, we preferred to use values for response likelihood, response distance and broadcasting time from the literature, instead of using values specifically established during this study for lions, because previous studies showed that the response of hyenas to calling stations (e.g. response distance) is considerably different from the response of lions (e.g. Maddox 2003).

Data analysis

The statistical analyses were performed using the software R 2.13.0 for Windows (R Development Core Team 2011), unless otherwise specified. Throughout the text, the term 'presence' (respectively 'absence') refers to whether at least one individual approached the calling station; the term 'abundance' refers to the number of individuals that approached. The response variable 'presence' was analysed for all calling station sites, whereas the response variable 'abundance' was only considered for those sites where at least one individual approached.

In a preliminary analysis we calculated Spearman's correlation coefficients between six candidate geographical predictor variables: distance to water, distance to the fence, distance to camps/lodges, percentage of floodplains, percentage of mixed sandveld and percentage of mopane woodland (Table S5). To avoid collinearity problems we excluded mixed sandveld and floodplains (see Supl. Mat. for further explanation).

We analysed the response of hyenas and lions to the calling stations, using generalized linear mixed models (GLMM) in GenStat (GenStat Sixteenth Edition 2013), with a Binomial and Poisson distribution assumed, respectively, for the response variable presence and abundance. Species (hyena and lion), season (dry and wet), type of call (hyena calls and lions calls), percentage of mopane woodland within a 3 km radius around each station, distance to perennial water, distance to lodges/camps, distance to fence and year were treated as fixed explanatory terms. Calling station identity, species within station and stations within season were retained as random terms for the analysis of presence/absence data. Calling station identity, species within station and type of call within station were retained as random terms for the analysis of abundance data. Model simplification of the fixed terms starting from a full model followed a backward-selection procedure based on the Akaike Information Criterion (Zuur et al. 2009). Start time and temperature at the beginning of each survey were also recorded and entered as single explanatory terms in analyses with presence and abundance of hyenas or lions as response variables. Neither start time nor temperature showed any relationship with the response variables, indicating that they did not introduce any biases in the data. Start time and temperature were consequently not included in the above GLMM models to reduce model complexity.

Although different broadcasting times were necessary for species-specific density estimates (30 min form hyenas and 60 min for lions), direct comparisons in the response of the two species to different types of calls required constant sampling time/effort. Therefore, when comparing the response of hyenas and lions to different types of calls, we only considered individuals that approached during the first 30 min of a 60-min broadcasting with lion calls. In this way we could compare, for example, the number of lions that approached the calling stations with hyena calls with the number of lions that approached the calling stations during the first 30 min of the lion calls.

Results

A total of 244 spotted hyenas and 67 lions were observed approaching the calling stations (Table 1). Over the entire study period, hyenas were recorded at 17 and lions at 9 of the 18 calling station sites (Table S6). Hyenas were observed at 71 (54.8 %) of the total 132 calling station surveys, while lions were recorded only on 22 (16.7 %) occasions (Table 1). The number of hyenas and lions approaching the calling stations ranged between 0–15 and 0–13 individuals, respectively, and varied between the 3 major habitat types (Table 1; Fig.

Table 1 Results of the response of spotted hyenas and lions to calling-station surveys in three habitat types: floodplains, mixed sandveld, and mopane woodland, with two different types of calls (hyena-focused vs. lion-focused)

	Spotted hyena		Lion	
	Presence (%)	Abundance (/station)	Presence (%)	Abundance (/station)
Floodplain ($N = 42$)	28 (66.7)	85 (3.0)	14 (33.3)	49 (3.5)
Hyena calls ($n = 19$)	13 (68.4)	52 (4.0)	5 (26.3)	9 (1.8)
Lion calls ($n = 23$)	15 (65.2)	33 (2.2)	9 (39.1)	40 (4.4)
Mixed sandveld ($N = 48$)	29 (60.4)	97 (3.3)	7 (14.6)	17 (2.4)
Hyena calls ($n = 24$)	14 (58.3)	65 (4.6)	0 (0.0)	0 (–)
Lion calls ($n = 24$)	15 (62.5)	32 (2.1)	7 (29.2)	17 (2.4)
Mopane ($N = 42$)	14 (22.6)	62 (4.4)	1 (2.4)	1 (1.0)
Hyena calls ($n = 19$)	6 (31.6)	38 (6.3)	1 (5.3)	1 (1.0)
Lion calls ($n = 23$)	8 (34.8)	24 (3.0)	0 (0.0)	0 (–)
Total ($N = 132$)	71 (53.8)	244 (3.4)	22 (16.7)	67 (3.1)
Hyena calls ($n = 62$)	33 (53.2)	155 (4.7)	6 (9.7)	10 (1.7)
Lion calls ($n = 70$)	38 (54.3)	89 (2.3)	16 (22.9)	57 (3.6)

"Presence" refers to the number of times individuals approached the calling stations and "Abundance" refers to the total number of individuals that approached the calling stations. The number in brackets represents the average number of individuals per calling station if only those calling station occasions where animals were observed were considered (='Abundance'/'Presence')

S2). Particularly striking was the relative absence of lions at calling-station sites in the mopane woodland, a sharp contrast to the number of lions approaching calling stations in floodplain habitats.

Only 4 of the 67 lions that approached the stations were individuals that had not previously been identified during the course of our larger research program. Of the 61 lions whose gender could reliably be determined 32 were males and 29 females, which translates in a sex ration of males to females of 1.10. This is in contrast to the sex ratio of males to females (adults and sub-adults) of 0.69 for the core study area in 2010. Males were present at 20 (90.9 %) of the 22 occasions where lions were recorded, while females only approached on 12 (54.54 %) occasions, and only on 2 of these 12 occasions did females approach unaccompanied by males. These figures suggest that male lions are generally more likely to respond to calling stations than females. Similar information could not be collected for hyenas due to the difficulty of identifying and sexing individuals in the field.

Calibration experiments: lion response time, distance and likelihood

We conducted 27 calibration experiments to measure the response time (and thus determine an appropriate broadcasting time for the main calling-station survey) and the response likelihood of lions (Table S4). The average time needed to approach the calling stations significantly increased with increasing distance from the loudspeaker and was significantly different between floodplains and mixed acacia sandveld (distance by vegetation interaction term, $F_{1,10} = 13.49$, $p = 0.006$; Fig. 2a). Whether time to approach varied between the mopane woodland and the other two vegetation types could not be determined because lions were only located on three occasions in this habitat type.

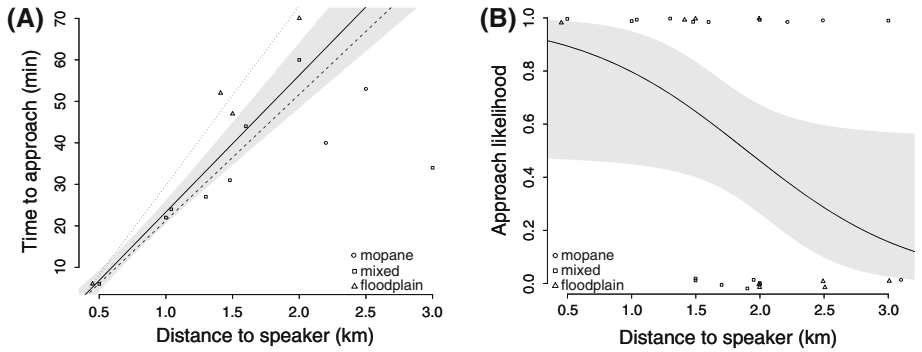

Fig. 2 Linear relationship (**a**) between the time taken to approach the speaker and the distance to the speaker for lions and logistic relationship (**b**) between the likelihood to approach the speaker and the distance to the speaker for lions. *Solid line* overall fitted values, *grey area* 95 % CI, *dotted line* fitted value for floodplains, *dashed lines* fitted values for mixed sandveld, *no fitted lines* are presented for mopane due to the limited sample size. Jittering has been introduced in **b** for the representation of the raw data (*open symbols*) to avoid overlapping data points

Averaged over all (including mopane) vegetation types ($n = 27$ experiments), time to approach was 56.3 min (CI 48.5–64.0) at a distance of 2 km (Fig. 2a). From this result, we concluded that a broadcasting time of 60 min was suitable to allow lions to within 2 km from the speaker (but not above this distance) to approach. When the distance from the speaker exceeded 1.5 km, the time to approach varied considerably, while it was almost perfectly linear below this threshold (Fig. 2a). This suggests that over longer distances the motivation to approach varied considerably, which also had direct consequences regarding the time taken to approach.

The likelihood of lions to respond to calls was investigated by logistic regression and analysed as a function of the distance to the speaker. Lions consistently approached if they were at a distance of less than 1.5 km from the speaker, while their response was less predictable beyond this distance (Fig. 2b; Table S4). Their likelihood to respond decreased significantly ($\chi^2 = 3.89$, $p = 0.02$) with increasing distance; and diminished from 0.9 at 500 m to 0.4 at 2.0 km (Fig. 2b). We used the results from the logistic regression depicted in Fig. 2b to calculate a mean response likelihood over the sampling range (0–2 km), which was $\mu_{Li} = 0.7$. This calculation was based on the assumption that animals were evenly distributed over the 2 km radius. We did not detect significantly different response likelihoods between the different vegetation types (either with mopane included or excluded in the analysis). In those cases where lions approached the speaker, on average 86.1 ± 7.3 % (mean ± SEM) of the focal individual(s) did approach (some individuals remained behind, particularly when retaining a kill; see Table S4). Assuming this value to be a constant over the entire response range, our results yielded an overall response likelihood for individual lions of $\mu_{Li} = 0.7 * 0.86 = 0.60$ at 2.0 km.

Presence and abundance

In a preliminary analysis, the spatial auto-correlative structure, among the 18 calling station sites, of the response variables presence and abundance was tested using Mantel statistics based on Spearman's rank correlation with 1,000 permutations and Euclidian

distances as similarity indices (Cozzi et al. 2008) following (Legendre and Legendre 1998). Hyena presence ($r = 0.01$, $p = 0.08$), as well as the number of hyenas approaching the stations ($r = 0.04$, $p = 0.14$) were not spatially auto-correlated, suggesting an even distribution across the study area. Lion presence ($r = 0.07$, $p = 0.03$), and the number of lions responding to the stations ($r = 0.18$, $p = 0.001$) were, however, significantly spatially structured. This spatial structure may have resulted from a corresponding spatial autocorrelation of the habitat types within the study site (see Fig. 1).

Spotted hyenas responded (response variable presence) significantly more to the calling stations than did lions ($F_{1,230.0} = 21.74$, $p < 0.001$; Table 1) and the two species' response was negatively affected by the amount of mopane woodland surrounding a calling-station site ($F_{1,29.7} = 5.86$, $p < 0.022$). The effect of mopane was highly dependent on season (interaction season by mopane $F_{1,23.5} = 7.66$, $p = 0.011$): both species showed a strong negative relationship with the percentage of mopane woodland during the dry season, while during the wet season no meaningful relationship was predicted by our model (Fig. 3). The presence of hyenas and lions at the calling-station sites furthermore marginally decreased with increasing distance to the closest lodge/camp ($F_{1,24.2} = 6.82$, $p = 0.015$), while we could not detect any significant relationship with distance to water and distance to fence. Our model did not detect significant differences between years, enabling us to rule out habituation events as possible source of bias in the presented results.

Significantly more (response variable abundance) hyenas approached the calling stations than lions ($F_{1,42.1} = 21.88$, $p < 0.001$; Table 1). The numbers of hyenas and lions arriving at the calling-station sites significantly depended on the type of call used to attract animals, i.e. hyenas responded more to hyena calls and lions more to lion calls (interaction species by call $F_{1,254.8} = 25.53$, $p < 0.001$; Fig. 4). After correcting for the effect of species and type of call used, we observed significantly more hyenas and lions approaching the calling stations the closer to lodges/camps ($F_{1,25.4} = 14.77$, $p < 0.001$), and the further to the veterinary buffalo fence that runs along the southern edge of the study area ($F_{1,23.9} = 6.15$, $p = 0.021$).

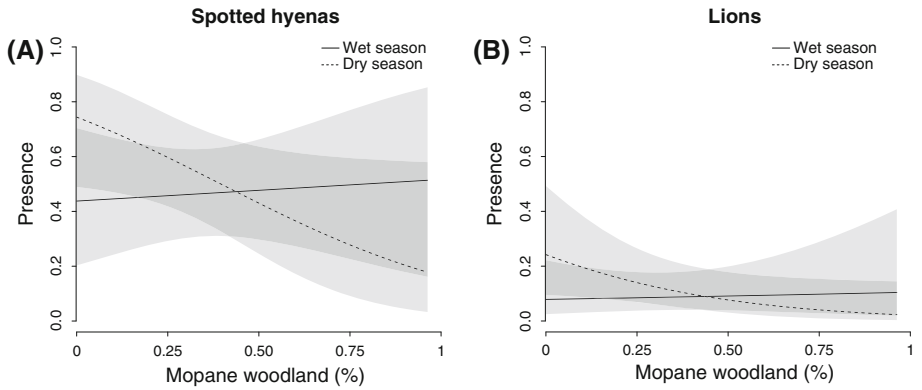

Fig. 3 Fitted values and 95 % CIs for the logistic relationship between the presence of **a** spotted hyenas or **b** lions and the percentage of mopane woodland surrounding a calling-station site within a radius of 3 km. *Solid line* wet season fitted values, *dashed line* dry season fitted values, *grey area* 95 % CI. For this graphical representation distance to camp has been set to be equal to the mean distance between the stations and the closest camp and distance to the fence to be equal to the mean distance between the fence and the stations

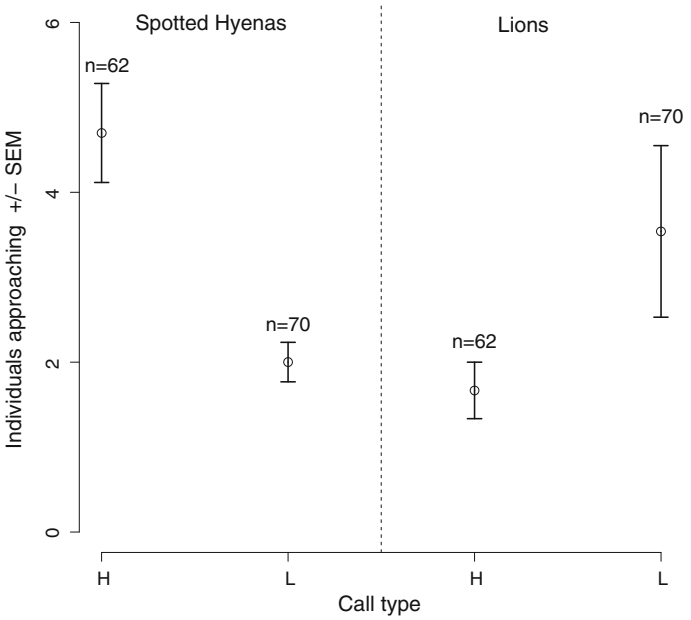

Fig. 4 Mean number of spotted hyenas and lions approaching the calling stations as a function of the type of call used. *H* hyena calls, *L* lion calls, *SEM* standard error of mean. Sample size is reported above *error bars*

Validation of calling-station survey by means of GPS radio-collars data

The percentage of each of the 3 major habitat types within the core study area of 980 km^2, where a total of 14 lions and 15 spotted hyenas were fitted with GPS radio collars, was compared with the percentage of the recorded GPS fixes within each vegetation type. Floodplains, mixed sandveld and mopane woodland represented, respectively, 11, 62 and 27 % of this core area. For lions, 8, 76 and 16 % of the GPS fixes collected ($N = 43{,}129$) were recorded within floodplains, mixed sandveld and mopane woodland, respectively. For spotted hyenas ($N = 33{,}297$ fixes), the corresponding values were 3, 75 and 22 % (Fig. S1). These trends obtained using GPS collars validate the results from the calling-station surveys, which show the tendency of lions to avoid mopane woodland and to intensively use floodplains, and the tendency of hyenas to be fairly evenly distributed across habitat types (with the possible exception of heavily inundated floodplains).

Estimating densities for the study area

Using information on the number of individuals approaching the calling stations, the distance at which animals approach (within a given broadcasting time) and the likelihood of approach, we were able to calculate densities for the study area and for the different habitat types (Table 2). Spotted hyena density showed little difference between the three habitat types with 16.9, 16.7 and 12.3 adults/100 km^2 for floodplains, mixed sandveld and mopane woodland, respectively. Weighed for the proportion that each habitat type represents within the survey area of 1,800 km^2, these figures give an overall hyena density of 14.4 adults/100 km^2.

Table 2 Spotted hyena and lion density estimates as a function of type of call and habitat type

Species	Type of call	Habitat	Density estimate (/100km2)
Spotted hyena	**Hyena calls (N = 62)[a]**	**Overall**	14.4
		Floodplain	16.9
		Mixed	16.7
		Mopane	12.3
	Lion calls (N = 70)[b]	Overall	4.7
		Floodplain	8.4
		Mixed	4.9
		Mopane	3.9
Lion	**Lion calls (N = 70)[c]**	**Overall**	5.8
		Floodplain	23.1
		Mixed	9.4
		Mopane	0.0
	Hyena calls (N = 62)[d]	Overall	1.5
		Floodplain	9.6
		Mixed	0.0
		Mopane	1.1

Overall densities for the 1,800 km^2 study area weighted by vegetation type are also reported. All calling-station occasions (N = 132) have been considered as independent data points (averaging numbers per station did not change the estimates and the data are not presented here)

The parameters used to calculate densities are as follow: [a] Response time: 30 min; response distance: 2.93 km; response likelihood: 0.6 (taken from the literature); [b] Response time: 30 min; response distance: 2.93 km; response likelihood: no correction for response likelihood since no calibration experiments on hyenas with lion calls were done; [c] Response time 60 min; response distance 2 km; response likelihood 0.6 (parameters from this study); [d] Response time: 30 min; response distance: 1.25 km; response likelihood: no correction for response likelihood since no calibration experiments on lions with hyena calls were done. Bold figures are given to allow comparison with other studies (e.g. Winterbach et al. 2002)

In contrast, the density of lions differed considerably between habitat types ranging from an almost complete absence in mopane woodland to an estimated density of 23.1 individuals/100 km^2 in floodplains (Table 2). Weighted for the proportion that each habitat type represents within the survey area of 1,800 km^2 and the core area of 980 km^2, these figures translate into an overall density of, respectively, 5.8 and 8.4 individuals/100 km^2. This difference has to be attributed to the higher percentage of mopane within the expanded survey area compared to the core area. Based on the lion densities estimated for each habitat type (Table 2) and the percentage that each habitat type constituted of the core area (11, 62, 27 % for, respectively, floodplain, mixed sandveld and mopane), a total of 82 individuals were estimated for the core area. For comparison, 76 individual lions were individually recognized through direct field observations during the course of our larger research program in 2010.

Discussion

We used calling stations, a relatively quick and inexpensive method, to survey spotted hyenas and lions in northern Botswana. Results allowed us to derive habitat-specific

density estimates for hyenas and lions in a 1,800 km^2 area associated with the Okavango Delta. We also identified seasonal differences in habitat use and the effects of different types of calls on the response of survey target species. In general, environmental factors (e.g. amount of mopane woodland surrounding a site) influenced the presence of animals at calling stations, while the type of call broadcasted was the primary factor influencing the number of individuals recorded.

Our lion density estimates were not directly comparable with the estimates by Winterbach et al. (2002) because, while our calling stations were stratified by habitat type, Winterbach et al. surveyed broader areas assigning to each area an overall uniform habitat type. Furthermore, differences between our estimates and the estimates by Winterbach et al. (2002) may reflect actual fluctuations in population density over the past 10 years. However some general conclusions can be drawn. Similar to Winterbach et al. (2002), our study showed relatively low lion density in large patches of mopane woodlands. Our lion density estimates on floodplains (23.1 lions/100 km^2) were higher than the values reported by Winterbach and co-authors (e.g. Survey area: high east; habitat: seasonal floodplain; density: min. 12.5 and max. 18.7 individuals/100 km^2, after correction for 60 % response likelihood).

These different results may be attributed to three potential methodological differences. First, Winterbach et al. (2002) considered a sampling radius of 3 and 4 km for their maximum and minimum estimates, respectively. They used a broadcasting time of 90 min, which, based on our results, seems appropriate for a sampling radius of 3 km (see Fig. 2a) but not for 4 km. This could have overestimated the area sampled resulting in low densities. Our values for response distance and likelihood were more consistent with values presented by Ogutu and Dublin (1998) (response likelihood of 25 % at 2.5 km), corresponding to an area with a radius of 2–2.5 km around calling stations for a broadcasting time of 60 min. Second, the types of calls broadcasted by Winterbach et al. (2002) did not include lion vocalizations and thus differed from the calls used in this survey. It is worth noting that our floodplain lion density estimate with hyena calls (9.6 individuals/100 km^2 before correction for response likelihood, see Table 2) matched the estimates by Winterbach and co-authors (Survey area: high east; habitat: seasonal floodplain; density: min. 7.5 and max. 11.2 individuals/100 km^2, before correction). However, to achieve the estimated density of 23.1 lions/100 km^2, a response likelihood of 23.1/9.6 = 0.4 (and not of 0.6) should be considered for hyena calls. Third, because of logistical constraints (limited roads and the inaccessibility of areas due to flooding) we could only survey about 13 % of the study area, less than the recommended 20 % of the total area suggested by (Ogutu and Dublin 1998). The relatively limited sample size may have introduced uncertainty into our results.

Overall, despite the slight discrepancies, the two studies showed fairly comparable results, confirming that the calling-station survey is a quick, efficient and accurate method to estimate densities of vocal territorial species. The similarity between the number of lions estimated for the core study area (82 individuals) and the number of lions individually recognized (76) further reinforced the reliability of the method and the accuracy of our estimates.

No hyena densities have previously been estimated for the Okavango Delta and no comparison was therefore possible. However, our estimates of 16.9, 16.7 and 12.3 hyenas/100 km^2 for, respectively, floodplains, mixed sandveld and mopane woodland obtained with the calling-station method are consistent with densities from other study sites showing a comparable prey base and vegetation structure, such as the Kruger National Park in South Africa (Mills et al. 2001; mopane woodland: 11.9 hyenas/100 km^2, mixed sandveld: 21.1

hyenas/(100 km^2) and in the Selous National Park in Tanzania (Creel and Creel 2002; 30 adult hyenas/100 km^2). Nonetheless, we acknowledge the need to conduct calibration experiments on hyenas in the study area to verify whether response distance and response likelihood values from the literature entirely apply.

Our results showed that lion distribution and density varied considerably among different habitat types, while spotted hyenas were more homogeneously distributed throughout the study area. We recorded the highest number of lions approaching the calling stations in prey-rich areas in floodplains and the associated riparian woodlands and grasslands (see Table 1; Fig. S2), where the estimated density was comparable with values in prey-rich areas of eastern Africa (Ogutu and Dublin 1998). On the other hand, the near-zero density of lions in mopane woodland was likely a result of the low density of prey species in that habitat. We concluded that large areas of mopane woodland represent a suboptimal habitat type for lions and that they may mainly use edges, particularly during the wet season (Fig. 3) when relatively more prey species are present (Bartlam 2010; Broekhuis 2012). These results are consistent with previous studies showing a direct relationship between the abundances of lions and their prey species (Ogutu and Dublin 1998, 2002; Carbone and Gittleman 2002; Hopcraft et al. 2005). Similarly, spotted hyenas were recorded at lower densities in the mopane woodland during the dry season, coincident with the lowest number of prey species (Bartlam 2010), thus supporting the positive association between hyenas and prey species reported elsewhere (Cooper et al. 1999; Trinkel et al. 2004; Höner et al. 2005).

Location data from animals fitted with GPS radio collars confirmed the relatively low use of mopane woodlands by the two focal carnivore species in this study, particularly lions (see also Cozzi 2013, pp. 94–95). Mopane represented 27 % of the core study area, while only 16 % of the lion locations and 22 % of the hyena locations where within this habitat type. Although lions sometimes transit through mopane (Fig. S1–S3), large patches of mopane may limit territory expansion of lions. Mopane woodland characterizes vast areas of northern Botswana and the low lion density in this habitat must be taken into account when extrapolating density estimates derived from different habitats to establish population estimates for broad landscapes. Other predator species whose density is not directly linked to prey density (Mills and Gorman 1997) and which suffer from direct predation and competition by lions, such as the African wild dog *Lycaon pictus* (Creel and Creel 1996), may consequently find spatial refuge in the prey-poor mopane woodland.

There appeared to be a discrepancy between the result of the calling-station survey, which pointed out floodplains as a preferred habitat for lions, and the GPS location data, which hint toward a marginal avoidance (floodplains represented 11 % of the core study area but only 8 % of the lion locations where in floodplains). It must, however, be emphasized that very large portions of floodplains were inundated all year round and therefore, despite included in the overall 11 %, not accessible to the animals (for more details on the effect of water bodies on lions and hyenas see Cozzi et al. 2013), which concentrate on seasonal, dry floodplains or in other habitat types in the immediate vicinity of water. In fact, all floodplains calling-stations, where we recorded a high lion response, were characterized by a high percentage of dry habitats (in the specifics mainly mixed acacia woodlands; Table S2) within a 3 km-radius.

The absence of lions responding to the floodplain calling-station site adjacent to the veterinary buffalo fence that runs along the southern edge of the study site (Fig S2, bottom left) could have resulted from a reduced response rate due to direct persecution on the south (pastoralist) side of the fence, where one case of farmers shooting one female lion is known to the authors. Similarly, the effect of human-induced mortality along the edges of

protected areas (Woodroffe and Ginsberg 1998; Loveridge et al. 2007; Balme et al. 2010) may explain the positive relationship between the number of animals recorded at the calling station sites and the distance to the fence. The observed pattern was, however, mainly driven by one single calling station site, the furthest most, where a total of 22 lions were recorded over time (for comparison, 10 or less individuals were recorded at all other sites). We therefore caution from over-emphasizing the concept of edge effects to this specific study. However, we encourage further investigation on the effect of the fence in particular, and human activities in general on lion and hyena populations. For example, as suggested by the positive relationship between responses to calling stations and the distance to lodges/camps, lions, and particularly hyenas, may even profit from human-related activities and food sources such as refuse dumps, which have been shown to influence the distribution of the latter (Kolowski and Holekamp 2008; Yirga et al. 2012).

Our results suggest that different types of calls attract animals differently and highlight the need to have a standardized set of calls, which depend on the target species to be surveyed (Kiffner et al. 2007). During the calibration experiments, we observed that lions responded noticeably to the 'lioness roar' (lions repeatedly lifted their head every time the lioness was broadcast, while they often ignored all other playback sounds) and we therefore consider this playback sound critical. When creating our 'hyena calls' and 'lion calls' we assumed that the distress calls of different species (e.g. wildebeest and buffalo) would equally attract hungry carnivores. We acknowledge, however, that different sized prey species could differentially attract hyenas and lions and we suggest further investigation. While we assumed that broadcast calls would spread equally between different habitat types and that the response would therefore be constant (an assumption corroborated by the fact that in our calibration experiments we did not detect significant differences in the response likelihood between the three different habitats), further observations are needed to investigate sound attenuation within different vegetation types. Nevertheless, the relatively limited response radius that we used for our calculations (2 km) leads us to believe that we were sampling well within the maximum audible distance for each vegetation type.

While reviewing the literature, we observed an inconsistency in broadcasting volume among the various studies. Some studies did not report the broadcasting volume (Mills et al. 2001; Winterbach et al. 2002), some played calls at "maximum volume" (Ogutu and Dublin 1998; Kiffner et al. 2007) and some at 103 dB (Creel and Creel 2002). Given that the dB scale is a logarithmic scale (for example, a 3 dB change corresponds to about a twofold change in power ratio) a difference of a few dB corresponds to significant changes in volume with substantial differences in the area surveyed.

These examples show that there is an urgent need to standardize calling-station methods to allow for comparisons between years and among different study areas, and to avoid misleading conclusions. On the basis of previous studies (Ogutu and Dublin 1998; Mills et al. 2001; Creel and Creel 2002; Winterbach et al. 2002; Kiffner et al. 2007; Graf et al. 2009) and our own results we can make six recommendations to survey lions and spotted hyenas: (1) a standardized set of calls, specific to each species, should be developed by scientists active in this field of research. The calls used during this study are a collection of calls used in past studies (e.g. Mills et al. 2001; Creel and Creel 2002) and may be suitable for standardisation purposes. To survey hyenas and lions simultaneously (thus maximizing financial effort and time), the same set of calls containing calls of prey in distress and social cues of both species may, however, be used. Yet, because hyenas and lions respond differently to different calls (this study), calibration experiments will need to be conducted for both species separately and the values suggested below at #4 may not apply. (2)

Response likelihood, response distance and response time should be investigated separately for different habitat types and across different seasons. (3) Because the response likelihood varies over the sampling range, decreasing with an increasing distance from the speaker, average response likelihood across the entire sampling range needs to be calculated. (4) An adequate broadcasting time should be matched with a specific sampling radius (broadcasting time and sampling radius are a function, respectively, of the response time and response distance assessed through calibration experiments). Where calibration experiments to determine site-specific broadcasting time and sampled radius are not possible and if the calls used are comparable to those used in this study, a broadcasting time of 60 min and a sampled radius less than 2.5 km should be used when surveying lions. Broadcasting time should be 30 min and the sampled radius 3 km when surveying spotted hyenas. Although we did not conduct calibration experiments on hyenas, data from the calling-station surveys showed that the mean time required by the first hyena to approach a calling-station using hyena calls was 11.2 ± 1.7 min (mean $\pm$ 1 standard error of the mean), thus confirming that a broadcasting time longer than 30 min may be unnecessary. (5) The sampled area calculated with these radii should include at least 20 % of the study area. (6) Broadcasting volume should be standardised at 110 dB. This volume is well within the natural pressure levels of the two species (Durant 2000; Webster et al. 2012), is easily achieved by readily available modern equipment (speakers and amplifiers) and the sounds is audible by both species at 3 km.

Due to increasing human population sizes and human pressures on resources, wildlife is increasingly forced into smaller areas with more severe boundaries, increasing the need to actively manage valued wildlife resources. Reliable population estimates for top predators in different regions and habitat types is paramount to the development of management action plans. Results from this study emphasise the importance of standardizing survey methods to enable reliable comparison of multiple surveys by avoiding intrinsic sources of uncontrolled variance in the calling-station method, a method that is increasingly used for monitoring purposes and which is providing results upon which conservation and management decisions and practices are being based.

Acknowledgments We thank the Botswana Ministry of Environment, Wildlife and Tourism and the Botswana Department of Wildlife and National Parks for permission to conduct this study. This research was conducted under research permit EWT 8/36/4. We thank G. Mills, K. McComb and P. Viljoen for kindly providing the recordings used during playback surveys. H. Webster helped with the experimental design, C. Winterbach and two anonymous reviewers provided valuable comments on an earlier version the manuscript. O. Sonzogni and the research staff at the Botswana Predator Conservation Trust assisted in the field. P. Barnett's editing is greatly appreciated. The study was funded by the Basel Zoo, the Forschungskredit of Zurich University, the Vontobel Stiftung, and numerous private donors through the Botswana Predator Conservation Trust.

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